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The Anterior Cranial Nerves
of Chelydra Serpentina

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THE ANTERIOR CRANIAL NERVES OF
CHELYDRA SERPENTINA

BY

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A. B. George Washington University, 1913.

THESIS

Submitted in Partial Fulfillment of the Requirements for the

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY

Mr. Frank Blair Hanson

ENTITLED

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Chelydra serpentina

BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE

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I

INTRODUCTION

In the fall of 1913 Professor J. Sterling Kingsley called my attention to the fact that the subject of cranial nerves in the reptiles is an almost virgin field for investigation. Upon looking over the literature I found but little on the general field of reptilian cranial nerves, and practically nothing on the turtles. Fischer (52) covers the whole field in a general way. Bojanus (1819) is still the classic work on the anatomy of the turtle. Watkinson (06) on Varanus and Ogushi (13) on Trionyx complete the list of important papers in this field. All of the above mentioned work was done by gross dissection methods and no attempt was made to determine anything concerning the nerve components.

Bojanus, Humphrey, and Ogushi have described and figured the brain of Chelydra. They are in such substantial agreement that I accept their results and in this paper will not touch upon the brain except in so far as is necessary to indicate the origin of the different cranial nerve roots.

I desire to thank Professor J. Sterling Kingsley for his interested and helpful criticisms during the progress of this investigation.

II

MATERIAL AND METHODS

This work was done with embryos of *Chelydra serpentina* which were secured from Dr. George W. Meyer of Oconomowoc, Wisconsin. An embryo nine millimeters long was found to be too young, but in an embryo measuring thirteen millimeters the development of the cranial nerves had reached approximately an adult condition. Several series of transverse sections were made, the stains used being Delafield's haematoxylin with eosin and alum cochineal with Lyons blue. The latter stain was found to be the better one for tracing nerve distributions. The sections were cut fifteen and twenty micra thick and the nerves were plotted on millimeter paper.

III

DESCRIPTION OF CRANIAL NERVES

I. NERVUS OLFACTORIUS

A. Nervus olfactorius.

B. Nervus terminalis.

C. The organ of Jacobson.

A. Nervus olfactorius.

The nervus olfactorius is the largest in diameter and the shortest of all the cranial nerves. It extends from the anterior end of the rhinencephalon to the olfactory epithelium. It arises by two roots, a ventral and a dorsal, called by Bojanus (1819) ramus externus and ramus internus respectively. Ogushi (1913) describes the ramus internus as the dorsal and larger branch of the two. Dorsal it is, but it is not the larger branch (fig.1). Ogushi had access to the work of Bojanus and claims to confirm his account. But Bojanus shows (fig.87) the ramus internus, the smaller branch, to arise dorsally and later to cross ramus externus ventrally before the distribution of fibres takes place. After this crossing, according to the figure of Bojanus, the dorsal branch is the larger one, but it is ramus externus and not ramus internus.

Both Bojanus and Ogushi relied entirely upon a study of the gross anatomy of the nerve. I have several good series of transverse sections and in all the ramus internus is the smaller branch. It arises from the dorsal and medial side of the bulbus olfactorius and retains this medial position throughout its length and its fibres are distributed to the inner or medial side of the nasal organ. In transverse sections I am unable to find any such change of positions of the two main branches of nervus olfactorius as Bojanus figures and Ogushi corroborates. The bundle of fibres

from each root remain distinct through their course. Figure 2 shows the fibre bundles just before the nerve enters the nasal capsule. The ramus externus evidently supplies both the medial and lateral sides of the nasal organ, while the ramus internus supplies only the medial side.

After leaving the rhinencephalon the nerves pass anteriorly, keeping close to the cartilaginous septum narium. Immediately after passing through the fenestra olfactoria into the nasal capsule the nerve bundles break up into numerous branches, divide to right and left and proceed ventrally down the sides of the nasal organ, supplying the olfactory epithelium.

B. Nervus terminalis.

The nervus terminalis, first described by Pinkus (94) in *Protopterus*, has now been found in every group of vertebrates except the birds, having been found recently in man by Johnston (13) and Brookover (14). The only turtle in which the nervus terminalis has been reported is *Emys lutaria* (Johnston 1913). He found it to arise from the rostral end of the medial wall of the hemisphere, caudal to the olfactory bulb. It comes into close relation with the dorsal division of the olfactory nerve, and there is some mingling of fibres, but because of the ganglion cells distributed along its entire length (a fact observed by other investigators on different forms) he was unable to trace it to its distribution in the rostral portion of the medial diverticulum.

The same conditions are found in *Chelydra serpentina* as far as I have been able to go with the material at my command. My sections are not properly stained for tracing nerve fibres and I am unable to trace the nervus terminalis after the mingling of its fibres with those of the dorsal branch of the olfactory nerve. However, in its origin and course up to this point the conditions are

so similiar to those in *Emys lutaria* that I have no doubt as to the identity of this nerve. In figure 4 the root is shown just emerging from the brain, some distance caudal to the olfactory lobe. Figure 3 shows the two nerves lying between the hemispheres. In this position they travel cephalad until, as is shown in figure 3, they come to lie between the dorsal and ventral roots of the olfactory nerve. The descending dorsal root soon mingles its fibres with those of the nervus terminalis. This is as far as my observations of this nerve go at the present time.

C. The organ of Jacobson.

I do not find an organ of Jacobson in this form, nor am I able to find in the literature any account of this structure in the turtles. Weidersheim in his anatomy of the Vertebrates (09, p392) says -" Bei Krokodilen, Schildkroten, und Vögeln sind keine ausgebildeten Jakobson's'chens Organe nachgewiesen" - and this is probably correct.

II. NERVUS OPTICUS.

The nervus opticus is the second largest of the cranial nerves. It arises from the floor of the diencephalon, therefore its fibres within the brain must run caudally and dorsally to reach the optic lobes. There is an optic chiasma (fig.6), which, seen in a transverse section, appears to be a simple crossing over, but, as is well known the fine fibres of the optic nerves are so interlaced that they can be studied only in series of transverse and sagittal sections, which are properly stained for the work.

Leaving the chiasma, each nerve penetrates the thick dura mater, and passes through the foramen opticum. Proceeding in a ventro-cephalad direction the nerve crosses anteriorly to nervus oculomotorius and posterior to the ophthalmicus branch of the trigeminus nerve, and, later, dorsal to the bursalis muscle and ventral

to the retractor bulbi. It pierces the bulbus oculi on its ventral and medial side, and its fibres are distributed over the retinal layer.

Figure 5 is a transverse section of the nervus opticus approximately half way between its point of origin and entrance into the bulbus oculi. In its general form it is circular, but with laterally compressed sides. There has been some discussion in regard to the shape of this nerve in the different forms. Among the bony fishes the nerve is commonly of a broad, plicated, ribbon shape, consisting of three laminae (Herrick 99). Studnicka (96) states that in the turtles *Amayda* and *Emys* the nerve is flattened, forming a ribbon, and in *Emys* this ribbon is a bi-folded structure, while in the bony fishes there are three folds. His theory is that this is an adaptation to secure the proper nourishment of the nerve and he thinks this was brought about by a double folding in the case of the bony fishes, or a single folding in forms like the turtle, of a ribbon-like nerve. Contrary to this, Deyl (95) considered that the ribbon-like nerve was derived from a cylindrical nerve by the intrusion of connective tissue septa. Ogushi apparently casts doubt upon the presence of ribbon-shaped nerves in *Amyda* and *Emys*, but bases his opinion upon the constantly circular form of the nerve in *Trionyx*, not upon observations on the other forms. Ogushi's description of the shape of the nerve in *Trionyx* is undoubtedly correct, except that he does not mention the lateral compression. However, in this section (fig. 5) the nerve is cut across at a considerable angle to its longitudinal axis, and this has accentuated the amount of compression shown.

A deep groove or narrow slit (fig. 5) opens on the ventral side of the nerve and extends to its center. This divides the nerve into two incomplete halves. Ogushi mentions this, and

says, that it has nothing to do with the fold of Studnicka. Whether this be true or not, the greatly increased surface caused by the furrow seems to fit Studnicka's theory of an adaptation for nourishment.

The general outline of the transverse section shown in figure 5 is strikingly similiar to what a section through the optic stalk at an earlier stage would be. The optic stalk is an hollow outgrowth from the forebrain, with a deep ventral groove, the choroid fissure. If this hollow outgrowth with its ventral fissure were filled with nerve cells, the result would be not unlike the form of nervus opticus, and it is not so much a matter of surprise that the early workers made the mistake of thinking that the stalk itself was transformed into the nerve.

The nervus opticus is described by Ogushi as being S-shaped in its course. I have plotted the nerve twice and am unable to make it appear as Ogushi saw it. There does seem to be a greater length than is necessary for the distance to be traveled, and the nerve is slightly bent, but not enough to suggest the letter S.

III. NERVUS OCULOMOTORIUS.

This is the largest of the eye muscle nerves. It arises from the ventral surface of the mesencephalon, near the middle line and has but a single root. In the early part of its course it lies dorsal to the hypophysis. Taking a lateral and slightly ventral direction through the dura mater, it reaches a position median to the anterior end of the Gasserian ganglion. At this point the nerve is two thirds as large as this part of the ganglion. The ramus opthalmicus of the fifth nerve and oculomotorius now parallel each other in their anterior course until they come to lie on the median side of the rectus superior muscle, where the ramus superior is given off.

There are five branches of the oculomotor nerves and they will be described in the order shown in the following table, which is Watkinson's classification based upon that of Fischer.

A. Ramus superior to the rectus superior muscle.

B. Ramus inferior.

1. ramus ciliaris to the ciliary ganglion.

2. ramus to the rectus inferior muscle.

3. ramus to the rectus internus muscle.

4. 4. ramus to the obliquus inferior muscle.

A. Ramus superior.

The nervus oculomotorius divides first into two branches, a dorsal and a ventral. The dorsal branch supplies the rectus superior muscle, while the ventral or inferior branch consists of the remainder of the nerve, and supplies the ciliary ganglion, muscles recti inferior, internus, and obliquus inferior.

The ramus superior is a strong branch, which immediately turns dorsally and is applied for a time very closely to opthalmicus of the fifth nerve, but does not anastomose with it. Turning in a slightly lateral direction, it crosses between the ventral side of the trochlearis and the dorsal surface of ramus opthalmicus, and comes to the posterior border of the rectus superior muscle, which it penetrates deeply.

Herrick (99) says that in bony fishes the ramus superior divides into two branches immediately after its separation from the main trunk. One branch of coarse fibres goes at once into the belly of the muscle, while the other branch, composed of fine fibres, runs along the dorsal edge of the muscle to its insertion upon the bulbus oculi, occasionally giving off twigs into its substance. In Chelydra the nerve does not divide and can be followed as a single branch to the centre of the muscle before breaking up.

B. Ramus inferior.

1. ramus ciliaris.

This, the first to separate from ramus inferior, is a strong branch, but not nearly so large as ramus superior. It is really a double nerve, and comes off from the main trunk by two branches, one immediately behind the other and in this position they enter the ciliary ganglion on its medial and ventral border. A branch from the ophthalmicus division of trigeminus enters the anterior edge of the dorsal side of the ganglion, which lies dorsally to the bursalis muscle and ventral to the rectus superior muscle.

Both Bojanus and Ogushi find three ciliary nerves, but in my sections only two of these nerves can be traced from the ganglion. One is a strong branch, while the other is very slender. They pierce the bulbus oculi at a point a little posterior and ventral to the entrance of the nervus opticus.

2. ramus to the rectus inferior muscle.

The ramus inferior, after giving off the ciliary branch, continues a course ventral and medial until it lies upon the ventral surface of the rectus inferior muscle, not far from its point of origin. In crossing over the ventral surface of this muscle several fine rami are given off to it and become distributed among its fibres. These rami constitute the contribution of nervus oculomotorius to the rectus inferior muscle. This condition is very similar to what Watkinson found in Varnus.

3. ramus to rectus internus muscle.

Very soon after the fibres are given off to the rectus inferior, the main stem divides into two nearly equal branches, one of which turns sharply in a dorsal and medial direction and, traveling closely along the intraorbital septum, reaches the rectus internus muscle and spreads out fan-like over its surface. The other branch is:

4. ramus to the obliquus inferior muscle.

This branch takes a ventral and lateral course and reaches the medial edge of the obliquus inferior muscle, which it supplies.

IV. NERVUS TROCHLEARIS.

The nerves of this pair take their rise, by single roots, near the middle line on the dorsal side of the mesencephalon close to the boundary between it and the cerebellum. Because of the over-hanging cerebellum they are scarcely visible until they leave the side of the brain, giving at first sight the appearance of having a lateral rather than a dorsal origin. This is an exceedingly long pair of nerves, being twice the length of abducens, and considerably longer than oculomotorius. But with the exception of abducens they are the smallest in diameter of the cranial nerves.

The dura mater is very thick in this region and the trochlearis travels through it a distance of about two millimeters before piercing the membranous wall of the brain cavity. Once outside it takes the most lateral position in a group of nerves, including three branches of trigeminus and two of oculomotorius, which lie almost at right angles to the middle longitudinal line of the brain. It now takes a cephalad-median course, and completes an almost perfect half circle, the ends of its diameter being its root and a point just level with the optic chiasma.

In the latter part of the half circle it meets and forms an anastomosis with the medial branch of the ophthalmicus division of the fifth nerve. Whether there is an exchange of fibres, I am unable to say. McKibben observed the same thing in *Necturus* and thought that fibres from the fourth nerve were given off to the fifth, for he saw twigs of the latter nerve entering the obliquus superior muscle. Emerging from this anastomosis the nervus trochlearis still continues its course cephalad and slightly medial,

paralleling for a considerable distance the ophthalmicus branch of the fifth nerve, but passing between the rectus superior muscle and the wall of the brain cavity, while the ramus ophthalmicus passes lateral to the rectus superior muscle. After crossing the nervus opticus dorsally, a more direct cephalad route is taken until it comes to the obliquus superior, where it divides into two branches, one going on each side of the muscle. Ogushi claims that it also supplies an obliquus superior accesorius. My sections do not show this and his reference is the only one I have seen in the literature of such an muscle.

V. NERVUS TRIGEMINUS.

Nervus trigeminus springs from the lateral surface of the anterior border of the metencephalon as a single large root. It emerges from the brain cavity through its own foramen, called by Gaupp and Watkinson foramen prooticum, but by Ogushi, the foramen sphenoidale. This is accounted for in the following manner: The foramen is an opening between the distal end of the basisphenoid and the prootic bones. In one case the ventral bone (basisphenoid) lends its name to the foramen, in the other, the dorsal (prootic) renders this service.

The foramen is very large and on the inner half of it the root enlarges into the Gasserian ganglion. This is by far the largest ganglion to be found among the cranial ganglia of Chelydra. It is roughly an equi-lateral triangle in shape, with one of its lateral sides parallel to the middle line of the brain. The root enters the median posterior angle of this triangle, while the ramus ophthalmicus leaves the median anterior angle. The lateral angle gives rise to three branches, ramus maxillaris, ramus mandibularis, and a fine branch called by Watkinson, ramus to the depressor inferioris muscle.

Fischer and Watkinson describe the Gasserian ganglion as

a double structure or as two distinct ganglia; one large ganglion for the maxillaris and mandibularis branches and a smaller one for the ophthalmicus branch. Ogushi denies this, and claims that there is but one ganglion for all branches, but finds that some ganglion cells extend into the ophthalmicus branch. This statement I have verified in my own sections, and as shown on the plot, the ganglion cells are thickly distributed along this branch for a distance of one third of a millimeter, or to the point where the first branch is given off. But nowhere is there a division into two ganglia.

A. Ramus Ophthalmicus.

The ramus ophthalmicus is the smallest and most anterior branch to leave the Gasserian ganglion. As already stated above, it leaves the median and anterior angle of the triangular shaped ganglion and at once takes a position median to oculomotorius, and ventral (not dorsal as Ogushi says) to trochlearis.

As in Varanus, it lies close to the membranous wall of the brain cavity and is bounded on its lateral side by the columella. For some distance forward it parallels the nervus oculomotorius on its lateral side. Entering the orbit and reaching the distal end of the retractor oculi muscle, these two nerves pass between it and the membranous wall of the brain cavity with the oculomotorius nerve here slightly in the lead. The ramus ophthalmicus passes medial to the rectus superior muscle near its point of origin and dorsal to the nervus opticus, reaching a point near the septum narium. After the ciliary branch is given off, the ophthalmicus divides into two nearly equal branches which run along side by side in the orbit a distance of over a millimeter, after which they meet and unite again in a single stem. Traveling for a considerable distance in an anterior direction near the wall of the septal cartilage, it finally takes a position lateral to the nervus olfactorius and continues in this relation through out the remain-

der of its course. The following branches are given off by it.

1. Ramus palpebralis superior.

This is the branch known as the ramus frontalis by most authors, but changed to the ramus palpebralis superior by Ogushi, because he wishes to distinguish it from the same branch in other reptiles, which in them also supplies the skin of the fore part of the head. In *Chelydra* it is not so extensive as this, but is confined to the hinder part of the eye and the skin of the upper eyelid.

This branch arises very soon after ophthalmicus leaves the ganglion, so early in fact, that Hoffmann designated it as a fourth branch of the trigeminus nerve (Ogushi). It turns sharply dorsally and runs along the membranous wall of the brain cavity until it meets and forms an anastomosis with the trochlearis nerve. Ogushi's figure shows a fine twig running from the distal end of this nerve to the trochlearis, thus connecting the two. This is not verified upon a microscopical examination of the two nerves. The connection is clearly one of anastomosis between the main branches, and not through a connecting twig. Distally the nerve divides into two end branches as described by Ogushi; one remaining in the hinder part of the eye-ball, the other dividing again and spreading over the upper eyelids.

In very close proximity to the root of this branch there is given off another one about half the size of the first. It follows just behind ramus palpebralis superior and takes exactly the same course, except for the anastomosis with the main branch of the trochlearis. It enters the hinder part of the eye at the same point and apparently fuses with one of the branches of the ramus palpebralis superior. My conclusion is that the ramus palpebralis superior is a double nerve, as is the case of the ciliary branch of the oculomotorius. I do not find any mention of such a branch

in the literature, nor is the ramus palpebralis superior described as a double nerve.

2. Ramus ciliaris.

With the description of Ogushi concerning this branch I am in total disagreement. In the first place, he says that this branch, which he calls radix ciliaris longa, is two and one-half times longer than the branch from the oculomotorius nerve, which branch he calls radix ciliaris brevis. The conditions appear to me to be just the reverse. The nervus oculomotorius lies ventrally at some distance from the ciliary ganglion, while the ophthalmicus branch of trigeminus at this point lies closely medial to the ganglion with just the edge of the retractor oculi muscle between them. The double ciliary branch from the third nerve which enters ventrally, has entirely disappeared within the ganglion before the ciliary branch of the fifth nerve reaches it; not, however, on its hinder edge, but on the extreme anterior and medial edge. So extremely anterior, indeed, that in the very next section after its entrance, the breaking up of the ganglion into the ciliary nerves begins.

3. Ramus cutaneus frontalis.

This is a very fine branch. After separating from the main stem, in the posterior region of the nasal capsule, it turns directly dorsally, entering the "pre-frontal nasal bone" (Ogushi), and from this it spreads out over the top of the head. This is the branch, which in other reptiles is a part of ramus frontalis, which branch is known in Chelydra as ramus palpebralis superior, because of the separation here of palpebralar and cutaneus parts into two distinct rami.

4. Ramus lateralis narium.

Immediately after giving off the ramus cutaneus front-

alis the main stem of ophthalmicus divides into two equal parts. The lateral one of these enters the nasal capsule, and gives off a twig which apparently fuses with a branch of the olfactorius. Ogunshi says that no part of this ramus goes to the nasal epithelium. This twig, however, is much too small to see in a gross ^sdissection. The lateralis branch continues ventrally down the inner side of the outer wall of the nasal capsule, dividing into two branches, one of ^{which} penetrates the wall of the capsule and continuing in a ventral direction innervates the external nasal glands. The other branch, following close behind, also penetrates the wall of the nasal capsule and supplies the skin in the lateral region of the head. This is the ramus premaxillaris superior.

5. Ramus medialis narium.

This branch, which is equal in size to the ramus lateralis narium, enters the nasal capsule through the foramen olfactorium and takes an extreme medial position, close to the septum narium. On its journey through the nasal capsule it lies in such close proximity to several branches of nervus olfactorius that I am not always sure just which is the medialis branch. However, at the anterior end of the capsule it is plainly seen passing through the fenestra inferior and supplies the internus nasal glands and, later, in the region of the premaxillaris bones, innervates the skin of the extreme anterior end of the head.

B. Ramus Maxillaris.

The ramus maxillaris leaves the Gasserian ganglion from its lateral and anterior border and enters at once between the thick pterygoideus and capitis-mandibularis muscles.

1. Rami temporalis.

Very soon there are given off from the main stem several small branches, which, in the posterior orbital region, break up into fine fibres and radiate out over a considerable

surface in the temporal region.

2. Ramus lacrimalis.

Bojanus and Ogushi describe the innervation of the lacrimal gland by a fine branch from the ramus maxillaris. In Chelydra a lacrimal gland is not present. However, there is an Harderian gland and it is possible that the above mentioned workers confused the two glands. These glands were worked out by Peters (90), who found the Harderian gland to be present in the reptiles generally, but noted the absence of a lacrimal gland in the turtles.

3. Ramus recurrens to VII.

Fischer and Watkinson describe a very fine nerve fibre running from the ramus maxillaris back to the seventh nerve. In its course it follows closely the temporo-muscularis artery and joins the main branch of the facialis nerve just anterior to the origin of the chorda tympani. This recurrens branch is not reported in any turtle, but in my sections I followed a fine branch from the maxillaris back as far as the anterior side of the otic capsule, which resembled closely the ramus recurrens described above for Varanus. Owing to the smallness of the fibre and a break in the sections I was unable to trace it beyond this point. It appears possible that there is a recurrens branch in Chelydra.

4. Ramus infraorbitalis posterior.

The main stem of maxillaris curves in a medial and ventral direction, dividing into two nearly equal branches. These are known as the rami infraorbitalis posterior and infraorbitalis anterior respectively. The former of these nerves proceeds laterally and enters the alveolar canal of the maxillary bone.

Here an interesting observation on a possible bit of phylogenetic^{at} history was made. As is well known, the turtles have no teeth, yet at somewhat regular intervals there are given off

from this nerve small branches, which pass out of the maxillary bone through special canals and go to the place where teeth would occur if any were present. Seven such teeth-nerves were found in the upper jaw. Rose (92) observed in an embryo of *Chelone* midst the formation of the dental ridge, which, together with the nerves appearing in the embryonic stages of the turtle would seem to indicate a toothed ancestor.

5. Ramus infraorbitalis anterior.

This is the slightly larger and more medial branch of the maxillaris nerve. It almost immediately divides into two branches, one of which turns sharply medially and unites with the ramus palatinus of VII, as described in the account of the latter nerve. The other, the ramus infraorbitalis anterior, continues a direct cephalad course near the middle line, until it reaches the posterior region of the nasal organ. A branch given off at this point ramifies over the roof of the mouth. The main stem enters the anterior part of the alveolar canal and gives off at least one rudimentary tooth-nerve.

C. Ramus Mandibularis.

The ramus mandibularis is the first branch to leave the Gasserian ganglion. Its point of departure is from the posterior and ventral border of the ganglion. Continuing in a lateral direction for a short distance, it passes through the foramen sphenoidale and penetrates the thick masses of the temporal muscles. Turning cephalad it enters the alveolar canal of the mandibular bone, and is now known as the ramus alveolaris inferior. During its course a number of side branches are given off, which are described as follows:

1. Rami temporo-massetericus.

Ogushi has one short, thick branch arising near the base

of mandibularis, which immediately divides into fine branches and supplies the nearby muscles. In Chelydra these rami appear to come off from the main stem independently. The temporal, masseter, zygomaticus, and pterygoideus muscles all receive branches from this tuft of nerves near the origin of the ramus mandibularis.

2. Ramus recurrens buccalis.

This strong branch is given off from ramus mandibularis before the latter enters its bony canal in the lower jaw. Traveling laterally and ventrally it enters the bony canal in the os supra-angulare and emerges between the pterygo-mandibularis muscle and the skin covering the same. Passing posteriorly, it breaks up into a number of rami which innervate the skin nearly as far back as the columella. There is also an anterior, weaker branch, which innervates the skin covering the temporal muscle. Ogushi says that this nerve has been observed in all the groups of reptiles except Chelone. He identified it in Trionyx, and his description is fully verified. Watkinson describes it for Varanus under the name, ramus recurrens cutaneus. As indicated by this latter name it is entirely a sensory branch.

3. Ramus cutaneus externus.

After the ramus alveolaris inferior has entered the os mandibularis, there is given off a second recurrens branch. This passes closely around the Meckelian cartilage on its outer side and takes a ventral course between the skin and the mylohyoideus muscle, innervating the former. This branch has no connection with the ramus recurrens buccalis described above. Its posterior ramifications end near the point where the trunk of the last named nerve begins to break up into its side branches. This second recurrens nerve is not described by Ogushi for Trionyx. Watkinson, in addition to the regular recurrens branch, has a cutaneus branch

very similiar in origin and part of its course to this one, which which she calls the ramus cutaneus externus.

4. Ramus mylohyoideus.

The next branch to be given off is of considerable size and length, and leaves the main stem on its lateral side. It passes between the os dentale and Meckel's cartilage closely applied to the lateral side of the cartilage. Outside the canal its course is medial, and there are three distinct innervations of the muscle by this nerve. Two side branches are given off, which bury themselves upon the ventral side of the muscle, while the distal end divides into two parts, and each of these into twigs, which spread out over its anterior surface.

5. Ramus lingualis.

Soon after leaving the main stem this branch receives the chorda tympani of the facialis nerve as described under the latter. Near the point of fusion, two short, fine branches are given off, which innervate the mylohyoideus muscle near its point of attachment to the jaw bone. The ramus lingualis is a very long and fairly strong nerve. During its course a number of short rami are given off to the epithelium lining the lower side of the mouth. It finally passes into the tongue and ramifies over its surface.

6. Ramus cutaneus submentalis.

This branch separates from the main stem, but continues a short distance with it in the canal, then breaks through into the ventral part of the jaw and passing toward the median line supplies the skin of this region.

7. Rami dentales.

The ramus mandibularis during its course in the alveolar canal gives off five branches through special foramina, which proceed as if to innervate teeth. Seven of these rami were found in the upper jaw and their possible significance pointed out there.

VI. NERVUS ABDUCENS.

The nervus abducens is the smallest of the cranial nerves. It arises just posterior to the origin of nervus trigeminus, from the ventral surface of the myelencephalon and not far from the middle line.

In most of the lower vertebrates the nervus abducens does not arise as a single root. In the bony fishes Herrick generally finds this nerve to have two roots. Cole reports six rootlets in *Chimaera*, and McKibben, working on *Necturus*, finds several twigs uniting to form the main stem. Watkinson states that in *Varanus* it has but one root. In *Chelydra*, Bojanus and Humphrey describe the nervus abducens as arising by a single root, while Nick (12), and Ogushi, declare for two or more rootlets. In my sections, which are of a thirteen millimeter embryo and approximate closely adult conditions, there are clearly and distinctly two roots. They do not unite for some little distance after leaving the brain, but travel through the dura mater as they arose from the brain, one slightly posterior to the other.

After traversing a distance of one millimeter through the brain cavity the nerve enters its foramen in the basisphenoid bone. This opening is more in the nature of a canal than a foramen, for the nerve continues in it a distance of five sevenths of a millimeter before emerging, dorsal to the basis- pterygoid process and near the origin of the retractor oculi muscle. On the lateral surface of this muscle the nerve divides into two nearly equal branches, one, the ramus to the retractor oculi muscle turns sharply medial and pierces this muscle. The other or main branch is still applied to the lateral surface of the above mentioned muscle and traveling in a dorsal and anterior direction, next gives off a branch to the bursalis muscle, which lies just ventral to the retractor oculi muscle at this point. Both Bojanus and Ogushi failed

to observe this branch to the bursalis muscle, but Watkinson saw it in Varanus. The branch to the rectus externus muscle a little later pierces the bursalis muscle and breaks up into several small fibre bundles. As Watkinson describes the further course of this nerve the fibre bundles run parallel along the ventral surface of the muscle until they reach the rectus externus muscle, which they innervate near its middle point. My sections are stained with Lyons blue and I am only able to trace the fibres a short distance ^{after} they enter the bursalis muscle, but it is my belief that they leave this muscle and supply the rectus externus muscle in the usual manner.

VII. NERVUS FACIALIS.

The nervus facialis arises in the lateral line of the medulla oblongata in common with the root of the nervus acusticus. Its fibres are so closely bound together with those of the anterior branch of nervus acusticus as to be indistinguishable from it until the division of the latter into side branches. Leaving the anterior branch of acusticus it enters abruptly into the large, roughly triangular ganglion geniculatum. The nerve leaves this ganglion by two strong branches, one running directly cephalad, the other in a caudal direction. These two branches leave at right angles to the stem and run in opposite directions. The posterior one is called by Watkinson ramus hyomandibularis, and by Ogushi ramus posterior s. truncus hyomandibularis. The anterior one is known by Watkinson and others as ramus palatinus, but Ogushi does not describe such a branch at all. This omission is difficult to understand, for the anterior branch of the facialis nerve is fully as large, if not larger than the posterior branch and could hardly have escaped notice. The matter of its size and method of leaving the ganglion as above described agrees perfectly with what Watkinson observed in Varanus. However, Ogushi agrees with Bojanus in omitting this anterior branch. The figure



of Bojanus is very small and inadequate, but seems to fit Ogushi's description exactly. It would appear that in this case Ogushi relied upon and followed too closely the work of Bojanus, for there can be no doubt whatsoever as to the existence of this very large, strong branch which leaves the ganglion geniculatum and runs in an almost direct anterior direction. There can be no relation between this nerve and the thin, weak, hardly to be distinguished branch called by Ogushi *ramus communicans facialis cum nervo palatino*.

A. *Ramus Hyomandibularis*.

This branch leaves the ganglion at right angles to the root and proceeds at once in a caudal and slightly lateral direction. Passing ventrally to the ear capsule it comes to lie in the inner, ventral angle of *cavum intermedium*, not outer as Ogushi claims. Here a very small, hitherto unreported twig separates itself from the main branch, but is so delicate that even in sections it cannot be traced to any definite distribution.

Shortly before reaching the columella, the *ramus hyomandibularis* gives off its first side branch,

1. The *chorda tympani*,

which continues posteriorly for a short distance or until it nearly reaches the anterior side of the columella: then it bends forward, and next forward and inward, so that the columella lies very clearly behind this nerve. In *Varanus* (Watkinson) the nerve is given off a little farther back, but as it passes forward on the dorsal side of the columella, the morphological relations are practically the same. The *chorda tympani* after leaving *ramus hyomandibularis* travels in a ventral direction, passing near the posterior side of the *quadratum*, "penetrates the belly of the *depressor mandibulae* muscle" (Ogushi) and entering the dorsal side

of Meckel's cartilage pierces this cartilage and appears on its ventral and medial side. It retains this position while rounding the otic capsule and until nearly opposite the Gasserian ganglion, at which point it moves to the medial side of Meckel's cartilage and lies between it and the goniale. It continues this position in an anterior direction until it comes to the place where the lingual-branch of the mandibular nerve curves around the Meckelian cartilage and the two are fused.

Ogushi gives only a brief description of the course of this nerve, but devotes several pages to a discussion of the phylogeny, physiology, and anatomy of the chorda tympani, together with a review of the literature on the subject.

2. Jacobson's commissure.

After giving off the chorda tympani, the main stem passes dorsally over the columella and continues posteriorly as described by Ogushi and Watkinson. It then gives off Jacobson's commissure (*ramus communicans externus cum IX*). This is a small, short branch, which travels in a posterior and medial direction until it unites with the ganglion petrosum of glossopharyngeus. In Ogushi's account no mention is made of this trunk, neither is it figured by Bojanus.

3. Ramus digastrici.

The main stem in passing through the digastricus muscle divides into two nearly equal branches and each of these in turn immediately divides into two branches. The first of these four branches is the smallest, and almost at once passes into the digastricus muscle. This branch is described by Ogushi and named by him *rami musc. depressorum mandibulae*. He claims to have two branches of this nerve innervating the muscle, but a study of serial sections does not bear out this claim. Watkinson found but one branch in *Varanus*.

4. *Rami ad m. constrictorem colli.*

The lateral two of the above mentioned branches innervate the *m. constrictor colli*. In regard to the number of branches entering this muscle: Ogushi has but one, while Watkinson has two, and here again, the evidence of microscopical examination substantiates the work of Watkinson rather than that of Ogushi.

There is a distal continuation of the main branch of *ramus hyomandibularis* which is not mentioned by any worker on reptilian cranial nerves. This is the branch from which the *ramus* to the digastric muscle is given off. It passes through the last named muscle in a lateral and ventral direction and curves around the outer side of the first branchial arch to a still more ventral position. This is a very strong nerve and passes without side branches from the skull. My sections are of the head only and I am, therefore, at this time unable to tell anything concerning its fate in the trunk region. In its origin, and course as far as followed, it is strikingly similiar to the *ramus lateralis VII* of the amphibians, though of course no *lateralis* elements are present in *Chelydra*. Norris and Druner described this branch in *amphiuma* and agree that its fibres come mainly from the branch which earlier supplied the *depressor mandibulae* muscle-- and this is true also in *Chelydra*.

B. *Ramus Palatinus.*

The *ramus palatinus* is the anterior branch of the *facialis* nerve, and was overlooked by Bojanus and Ogushi, but the description by Watkinson for *Varanus*, with but few changes, would apply to *Chelydra*.

1. *Nervulus tympani.*

Almost before the nerve has left the *ganglion geniculatum*, a branch of moderate size is given off, which turns sharply

in a posterior direction, in company with the carotis internus, and unites with the ganglion petrosum. Shortly before its union with this ganglion, it receives a delicate twig from ramus hyomandibularis. It seems, as in Varanus, that this union with the ganglion is only partial and that the nerve continues again in a posterior direction. Ogushi discusses this branch under his description of nervus facialis, but says that the ganglion geniculatum receives the branch from ganglion petrosum rather than vice versa. This is the ramus communicans internus cum IV of Watkinson who says it is a branch given off from ramus palatinus which only partially unites with the ganglion petrosum, then leaves it again as the cervical stem of nervus sympathicus.

2. Rami communicans cum V.

After giving off the nervulus tympani, the ramus palatinus drops ventrally to a position on the lateral side of carotis internus and continues in this manner until immediately in front of the Gasserian ganglion. At this point it divides into two unequal branches, one of which is very weak and continues forward in company with carotis internus, innervating the palate in the sub-orbital region.

The other and larger branch takes a lateral and anterior course, uniting with the infraorbitalis branch of ramus maxillaris in the posterior orbital region. At the point of this union, several, short, fine twigs are given off to the surrounding tissue. Whether they contain elements of the V or the VII, or of both, I am unable to say. This branch, which unites the facialis and trigeminus nerves is called by Fischer "ram. com. post. c. ram. palatino", in order to distinguish it from an anterior connection between the same two nerves, which takes place in the anterior orbital region and is known by Fischer as "ram. com. ant. c. palatino".

VIII. NERVUS ACUSTICUS.

The seventh and eighth cranial nerves arise as a common trunk, one half a millimeter caudal to the root of nervus trigeminus. This is a very thick and short root, which pierces the dura mater and comes to a point on the medial side of the auditory capsule. Here it divides into two branches, called the anterior and posterior or ramus vestibularis and ramus cochleae respectively. The nervus facialis is so closely bound to the anterior branch that their fibres may not be distinguished until the two separate to go to their respective distributions.

A. Nervus cochleae.

This nerve turns in a caudal direction and passes through the foramen acusticum posterius. While yet in the foramen it begins to swell into the ganglion cochleae. This ganglion is very large and its cells extend along it until the division of the nerve into its respective branches takes place.

1. Ramus to lagena.

The first branch of this posterior part of nervus acusticus is a small one given off to the lagena. It enters the sensory organ of the lagena just after the separation of this part from the sacculus.

2. Ramus to sacculus.

The lagena lies ventral to the rest of the ear and nearest the foramen acusticum posterius. The main branch now takes a dorsal direction between the median wall of the cartilagenous otic capsule and the sacculus. While in this position the nerve divides into two nearly equal halves and the ventral one of these reaching laterally to the sacculus supplies its sensory parts.

3. Ramus to posterior ampulla.

This is the longest branch of the cochlear nerve. It

continues to run dorsally to a point between the sacculus and the utriculus, where it turns in a lateral direction, followed closely by the ninth cranial nerve which passes directly through the otic capsule. This ramus to the posterior ampulla after reaching the lateral part of the otic capsule continues caudally until it reaches the sensory area of the posterior ampulla.

B. Nervus Vestibuli.

This is the anterior branch of nervus acusticus. Its ganglion, the vestibulare, is inside the foramen acusticum anterius. This is the branch which carries with it the main stem of the nervus facialis. At this point they are indistinguishable from one another.

1. Ramus to sacculus.

This is a very short branch and is given off immediately after the division of nervus acusticus into its anterior and posterior parts. It passes through a special foramen in the otic capsule and is distributed over the medial side of the sacculus.

There are, therefore, two distinct branches innervating the sacculus of the Chelydra ear, one from the cochlear and one from the vestibular nerve. Hasse (73) does not mention this dual supply to the sacculus, but it is beautifully and accurately drawn by Retzius (84).

2. Ramus to the lateral ampulla.

This branch is given off from the ganglion while yet within the brain cavity. It passes through its own opening, called by Ogushi, acusticum anterius accessoria, while the opening for the main branch of the anterior part of nervus acusticus, he called the foramen acusticum anterius principale.

After entering the otic capsule this ramus turns slightly posteriorly and, passing between the sacculus and the utriculus, reaches the sense organ of the lateral ampulla.

3. Ramus to the utriculus.

Before this branch is given off the seventh nerve separates and passes into its ganglion. Then the main branch of *nervus vestibuli* passes in a lateral and anterior direction to the ventral side of the utriculus and supplies its sensory area; continuing cephalad, it becomes the,

4. Ramus to the anterior ampulla,

which lies in the extreme anterior end of the otic capsule. There are, therefore, seven branches of the auditory nerve present in a thirteen millimeter embryo of *Chelydra*. No branches to the *macula neglecta* or *papilla acustica basilaris* were found.

IV

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V

ABBREVIATIONS USED.

I	nervus olfactorius.
II	nervus opticus.
III	nervus oculomotorius.
III1	ramus to rectus superior.
III2	ramus to ciliary ganglion.
III3	ramus to rectus inferior.
III4	ramus to rectus internus.
III5	ramus to inferior oblique.
IV	nervus trochlearis.
V	nervus trigeminus.
V1	ramus ophthalmicus.
V2	ramus maxillaris.
V3	ramus mandibularis.
VI	nervus abducens.
VI1	ramus to retractor oculi muscle.
VI2	ramus to bursalis muscle.
VI3	ramus to externus rectus muscle.
VII	nervus facialis.
VIII	nervus acusticus.
IX	nervus glossopharyngeal.
X-XII	nervi vagus, accessorius, and hypoglossal.
a.a.	anterior ampulla.
c.g.	ciliary ganglion.
cl. n.	ciliary nerves.
col. au.	columella auris
c.t.	chorda tympani.
dr.	dorsal
g.g.	Gasserian ganglion.

g.p.	ganglion petrosum.
j.c.	Jacobson's commissure.
l.	lagna.
l.a.	lateral ampulla.
n. cut. front.	nervus cutaneus frontalis.
n. olf. d.	dorsal root olfactory nerve.
n.t.	nervus terminalis.
n.t. rt.	root nervus terminalis.
n. tym.	nervulus tympani.
n. olf. v.	ventral root nervus olfactorius.
op. ch.	optic chiasma.
p.a.	posterior ampulla.
pr. fr.	prefrontal bone.
r. alveo. inf.	ramus alveolaris inferior.
r. const. col.	ramus ad m. constrictorem colli.
r. cut. ex.	ramus cutaneus externus.
r. cut. s. m.	ramus cutaneus submentalis.
r. digast.	ramus digastricus.
r. hym.	ramus hyomandibularis.
r. infra. ant.	ramus infraorbitalis anterior.
r. infra. post.	ramus infraorbitalis posterior.
r. lat. nar.	ramus lateralis narium.
r. ling.	ramus lingualis.
r. med. nar.	ramus medialis narium.
r. my. hy.	ramus mylohyoideus.
r. pal.	ramus palatinus.
r. palp. sup.	ramus palpebralis superior.
r. pr. mx. inf.	ramus premaxillaris inferior.
r. pr. mx. sup.	ramus premaxillaris superior.
rr. dent.	rami dentalis.
r. rec. buc.	ramus recurrens buccalis.

rr. temp.	rami temporalis.
rr. temp. mass.	rami temporo-massetericus.
s.	sacculus.
sep. nar.	septum narium.
u.	utriculus.
vt.	ventral

FIG. 1

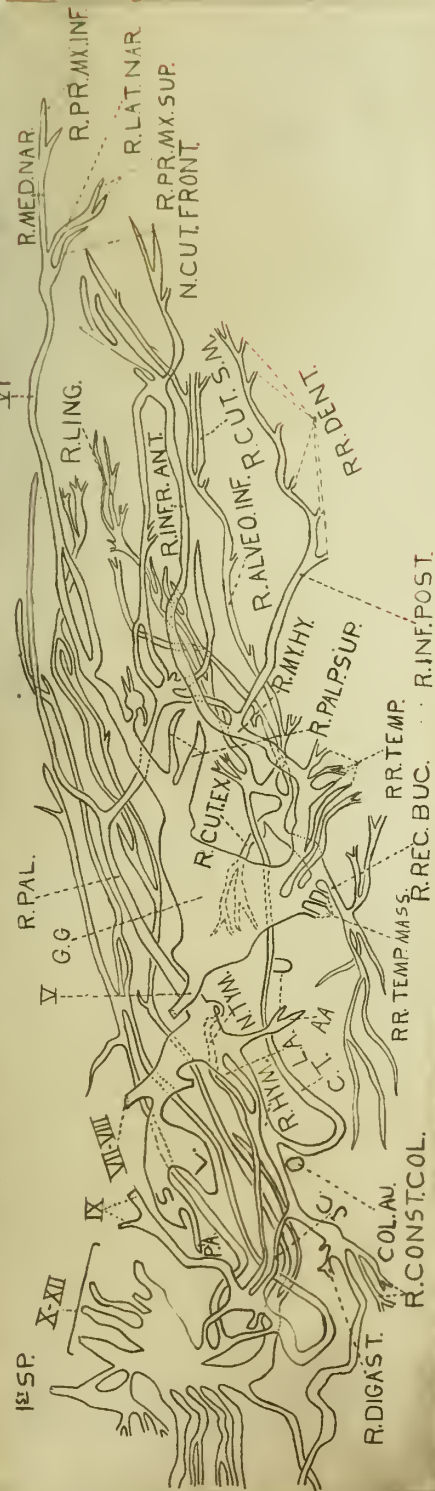


FIG. 2

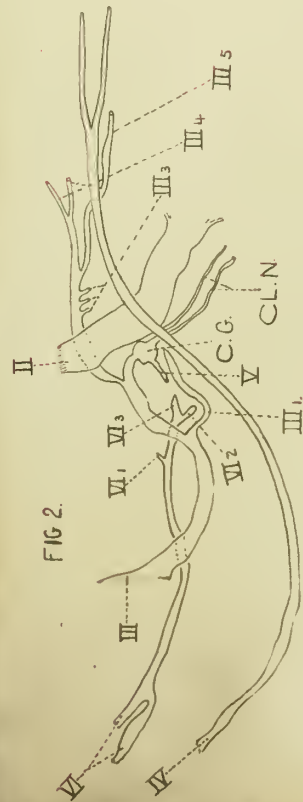


FIG. 3

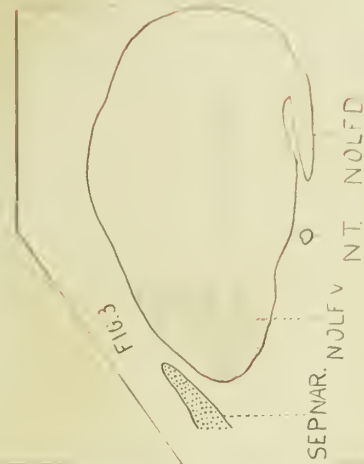
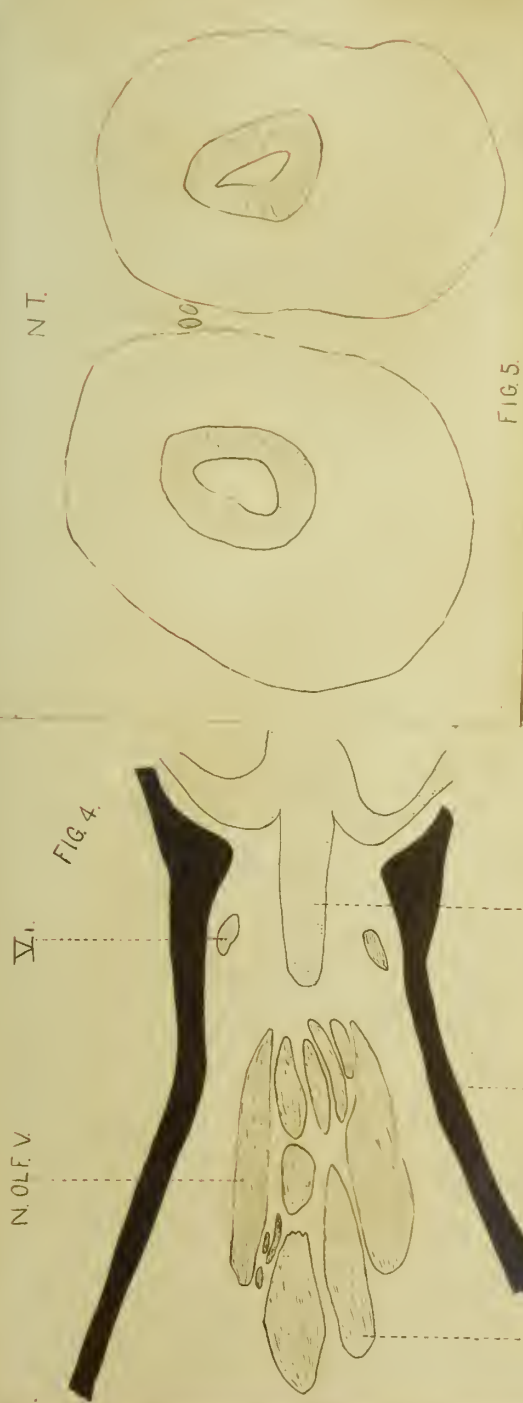
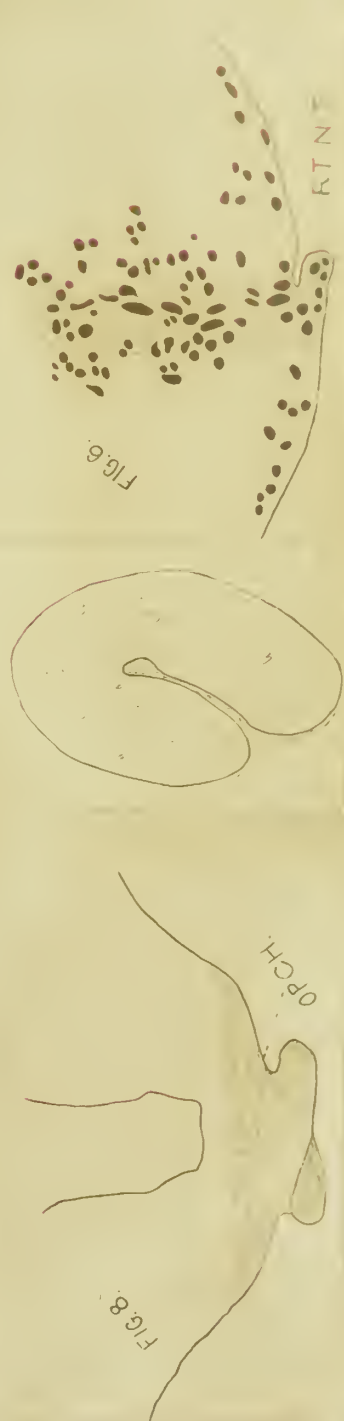


PLATE II.



NOLF D. PR' FR. SEP. NAR.

FIG. 7.







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